Plant–Environment Interactions

Second Edition

edited by

Robert E. Wilkinson

The University of Georgia
Griffin, Georgia

MARCEL DEKKER, INC. NEW YORK · BASEL

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Phytochrome in Crop Production*

Michael J. Kasperbauer
Coastal Plains Soil, Water, and Plant Research Center, Agricultural Research Service, U.S. Department of Agriculture, Florence, South Carolina

I. INTRODUCTION

Many plants are grown for their edible seeds; others are grown for their leaves, fruit, fiber, and ornamental value. Growth, development, and productivity of each plant is influenced by its genetics and the total environment in which it grows from seed germination through vegetative growth, floral induction, and seed development. The genetic component sets the plant's potential size, composition, and productivity; but environment determines the degree to which that potential is realized. The constantly changing growth environment includes soil moisture, mineral nutrients in the soil, air and soil temperature, insects, diseases, and light.

Of the environmental factors listed above, light at a given location follows a predictable pattern year after year. Therefore, it is reasonable that adaptation and survival of a plant is related to its ability to sense variations in the light environment as signals for seasonal growth events and for adaptation to competition from nearby plants. That is, a plant must be able to prioritize allocation and use of photoassimilate in developing growth patterns that favor survival long enough to produce its next generation of seed.

For many years, photosynthesis was thought to be the only contribution of light to plant growth and productivity. There have been many excellent laboratory studies of physiological mechanisms involved in the photosynthetic pro-

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cess, and field measurements of canopy interception of photosynthetic light have been studied extensively. Meanwhile, study of photomorphogenesis began rather slowly in the years leading up to the discovery of photoperiodism. Following the discovery of photoperiodism, photomorphogenesis was studied extensively in laboratories and controlled environments as a bioassay of photoreversible control of flowering and of various developmental events in growing plants, and this approach contributed to discovery of phytochrome.

After the discovery of phytochrome, it was initially assumed that phytochrome was the same in all plant species and in all ages of a given plant because of the similarities of energy requirements and action peaks obtained in controlled environments (1,2). An early objective was to determine the chemistry of phytochrome and its action at the molecular level in regulating plant processes. However, in subsequent years it became evident that there is a family of phytochromes with specific functions during a plant's life cycle. For example, Pratt and colleagues studied three oat (*Avena sativa* L.) phytochromes and found that a phytochrome that was most abundant in dark-grown seedlings was absent (or in very low concentration) in green seedlings (3,4).

Although the details are not yet resolved at the molecular level, it is evident that phytochrome plays a major role in a plant's ability to sense competition from other plants as well as to sense and respond morphologically to the changing seasons. It is evident that phytochrome is involved in sensing the total light environment and initiating physiological events that regulate allocation and use of the products of photosynthesis in a manner that improves a plant's chance of survival. A plant might be compared to a prudent investor. That is, it senses what is needed for its own survival (such as a taller stem if it is growing in competition with many nearby plants) and prioritizes investment of resources (especially the products of photosynthesis) to meet those needs; then it invests the resources not needed for its own survival to grow larger and produce more seeds to extend the next generation.

The recognition of phytochrome-regulated morphogenic responses to competition from nearby plants and to photon ratios in upward reflection from colored mulches in the field is built on information gained in many controlled-environment experiments and in some unexpected vegetative growth patterns in response to longer wavelengths of far-red on the Beltsville Spectrograph (5–7).

There have been many excellent review articles about phytochrome and photomorphogenesis in test plants (8–10). However, reviews of phytochrome action in crop production are limited. This chapter will summarize discoveries of photoperiodism and phytochrome, followed by development and use of information on phytochrome regulation of physiological processes in crop production. It will end by summarizing the development and use of colored mulch technology

in food crop production. Many of the examples used in the chapter are from the research of the author and his colleagues from the late 1950s to the present time.

II. DISCOVERY OF PHOTOPERIODISM

The discovery of a biological phenomenon is usually built on accumulated knowledge (or observations). For example, weed plants of the same species usually go through the same life stages at about the same time each year at a given location. It was also well known for many years by farmers that annual weed plants such as cocklebur (*Xanthium pensylvanicum* Wall.) could germinate and start growth at different times during spring and summer, but they would flower and develop seed at about the same time, as though something in nature told them when to flower so that their seed would ripen before freezing weather occurred. Of course, plants that started growth early frequently grew larger and produced many flowers and seeds, while the late-starting plants were only large enough to produce a few flowers and seeds. Nevertheless, both the early- and the late-starting plants did produce some seed to continue the next generation. The same principles of season recognition are involved in crop plants whose yields are affected by "date of planting."

When plants that were adapted to one geographic area were introduced into another area, time of flowering and other growth characteristics of the same genetic material frequently differed between the two geographic areas. This occurred when plants such as soybean [*Glycine max* (L.) Merr.] were introduced as a potential new crop. It also occurred when plants with desirable characteristics, such as disease resistance, were introduced into a plant breeding program in another geographic area. Again, there seemed to be influence of some environmental component that differed between the old and new geographic areas. Sometimes the introduced plants would flower early and produce few seeds per plant in the new geographic area. Other introduced plants would flower too late for seeds to ripen before freezing weather occurred. Such observations started W. W. Garner and H. A. Allard on the road to their classic discovery of photoperiodism (11).

Garner and Allard were U.S. Department of Agriculture (USDA) scientists who worked with the Maryland type of tobacco (*Nicotiana tabacum* L.) in the early 1900s at the Arlington Farm, close to where the Pentagon now stands. Research at that time was less specialized than it is today. Therefore, they were involved with a wide range of tobacco production problems including the development of new varieties that were resistant to diseases, grew better, and produced a high yield of leaf. The development of new genetic lines and varieties involved bringing some plants with desired characteristics from other locations and crossing them with the best of the locally adapted genetic lines

and varieties. Because the number and size of leaves per plant were important components of yield, they were interested in a genetic line that produced many more leaves than the standard varieties. The "giant" plants were observed as early as 1906 (11). Therefore, they wanted to cross plants of the giant line (later called "Maryland Mammoth") with some varieties and lines that had other desirable characteristics. Crossing these materials presented a problem because the giant plants did not flower at the same time as the others. An early hypothesis was that plants of the giant line had to be much older than the others before they were capable of switching from vegetative growth (leaf production) to reproductive growth (flowering). In an attempt to remove this problem, they moved some plants from the field to a greenhouse in autumn before freezing weather set in. The giant plants flowered in the greenhouse in winter and some cross-pollinations were accomplished with plants of the local varieties that were also in the greenhouse. Believing that they had solved the "age of responsiveness" problem, they started some seeds of the giant line in the greenhouse in late autumn so that the plants would be old enough to flower at the same time as the other lines and varieties after being transplanted to a field during the next growing season. The research plan seemed appropriate, but there was an unanticipated problem. Plants of the giant line that were started in late autumn in the greenhouse flowered at a small size and with few leaves per plant in the greenhouse in winter. It must be noted that greenhouse lighting was not a standard practice at that time, and the plants were grown in the greenhouse under natural winter day lengths at the Arlington Farm. Thus, the scientists were faced with a serious challenge. They had a tobacco line that produced many leaves (desirable) but flowered too late to cross with the other lines and varieties in the field. However, flowering was early and with few leaves per plant if they grew the giant line in the greenhouse in winter. Initially, they questioned whether the early-flowering response in the greenhouse resulted from using the wrong seed. However, when seed from the early-flowering winter plants of the giant line were grown in the field, they again produced giant (late-flowering) plants. That is, the genetic component had not changed and the early-flowering response was clearly related to some component of the environment.

Garner and Allard's experience with flowering of the giant line of tobacco caused them to wonder if length of day was the critical environmental factor. To test the theory, they moved potted plants into and out of "dark houses" at different times of day to break each long summer day into 2 or more short days. In winter greenhouse experiments, they compared plants grown on natural day lengths with others grown on natural days that were lengthened several hours by illumination from tungsten-filament lamps. They did similar experiments with soybean and Maryland Mammoth tobacco. Both species flowered earlier when given short days and later when given extended days. They concluded that length of day (or length of light period) was the environmental component

that was responsible for time of flowering. They coined the term *photoperiod* for the controlling factor and *photoperiodism* as the response to photoperiod in their classic paper on the discovery of photoperiodism, which was published in 1920 (11).

Following the discovery by Garner and Allard, many scientists throughout the world published papers showing that other plant species sensed photoperiod and used that environmental signal to initiate flowering. As the papers appeared, it became apparent that the photoperiod sensing mechanism was sometimes modified by temperature. Nevertheless, the knowledge allowed plant breeders to synchronize time of flowering of genetic lines from many different geographic areas (with different natural day lengths) and make the desired cross-pollinations. Suddenly, it was easy for plant breeders to extend the natural day lengths with artificial light in the greenhouse to get longer days and to use light-tight curtains or a nearby dark room to give plants shorter than natural day lengths. Horticulturists also used the knowledge of photoperiodic control of flowering, especially in the flower production industry.

After the term photoperiod (for day length) was firmly established in the scientific literature, it became apparent that the number of hours of uninterrupted darkness rather than the hours of light was the dominant factor involved in the timing mechanism (12). From a practical viewpoint, the problem of synchronization of flowering time was solved. But knowledge of the photoperiod sensing mechanism within the growing plant was yet to be resolved. The next major step in the research was based on the fact that a short period of darkness during the day did not affect flowering time, whereas a short period of light near the middle of the night delayed flowering of short-day plants and hastened flowering of long-day plants.

III. DISCOVERY OF PHYTOCHROME

A new USDA research team was organized at Beltsville, Maryland, in the mid-1930s to study the nature of photoperiodism and its significance to agriculture. The team consisted of Harry A. Borthwick (a botanist) and Marion W. Parker (a plant physiologist). Their objective was to identify the light-sensing mechanism involved in photoperiodic control of flowering and other aspects of plant development. They quickly confirmed that flowering of plants such as soybean and cocklebur was delayed if the plants received a brief exposure to white (a mixture of all colors) light near the middle of the night; a short period of darkness applied near the middle of day did not affect flowering time. This was followed by many experiments to determine effect of color of light near the middle of night, plant age, and even leaf age. At that point it was important to develop facilities in which to conduct this new type of research.

Two "photoperiod houses" similar to those used by Garner and Allard at the old Arlington Farm were constructed at Beltsville. Plants were grown in boxes mounted on carts and moved into and out of the buildings on steel rails. The buildings were equipped with electricity, and light-tight curtains were used to separate treatment compartments within the buildings. This allowed use of natural outdoor summer daylight alternated with various timing and light combinations when the plants were inside the photoperiod houses.

Some of the planned research required that brightness of the basic light period (the day) would not vary with season as it did outdoors, next to the photoperiod houses or in a greenhouse. In order to obtain such lighting for plant growth, the team used a carbon-arc lighting system, which was supplemented with white incandescent-filament lamps arranged in a circle around the carbon-arc in a room with temperature control (Fig. 1). The table used to support growing plants was also circular in shape and placed below the incandescent lamps. This lighting system was installed in 1937 (13); it was used successfully until 1963, when it was replaced by very high output (VHO) cool-white fluorescent lamps supplemented with incandescent-filament lamps (14). The carbon-arc growth room was instrumental in development of the 8-hr light period as the standard "short-day." This came about because the carbons would burn for

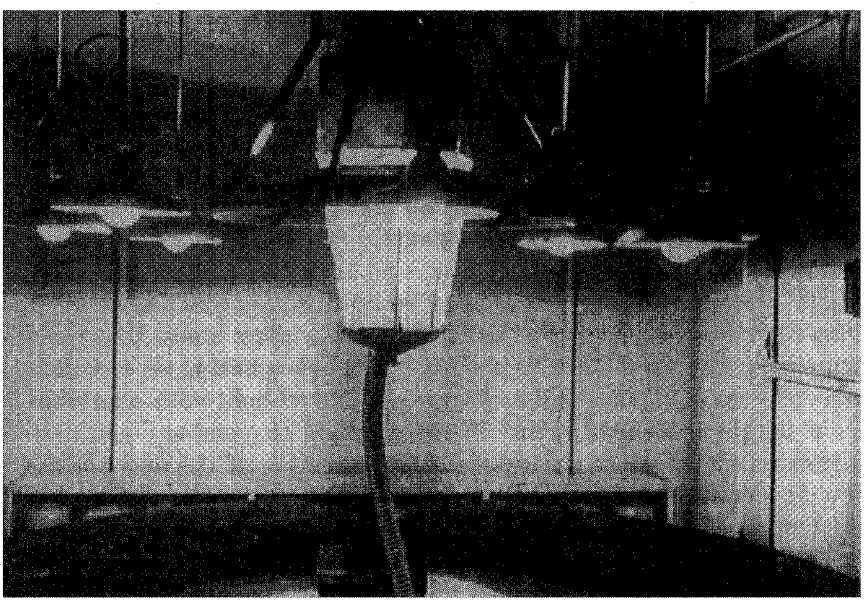


Figure 1 Carbon arc plant growth room used at Beltsville from 1937 to 1963. (USDA photograph.)

about 8 hr and 15 min before needing replacement. Therefore, many of the early growth-room experiments with soybean and cocklebur (both are short-day plants) involved 8 hr of the bright light and other light combinations given in adjacent rooms where the plants were treated with various colors, durations, and intensities of light during the 16-hr night.

Because more space was needed for larger experiments, some of the research was done in a greenhouse which was equipped with supplemental light sources in adjacent rooms. The potted plants were grown on 30×60 in. platform trucks rather than on fixed benches in order to allow more orderly movement to adjacent rooms for various supplemental light and temperature combinations during the night. The platform trucks were moved from daylight in the greenhouse into the adjacent rooms at 4 p.m., where they received their supplemental light and/or temperature treatment during the 16-hr night. They were returned to the greenhouse at 8 a.m. The same pattern was repeated each day for the duration of an experiment. These studies allowed treatment with various colors, intensities, and durations of supplemental light in addition to the 8 hr of natural light in the greenhouse.

Experiments were designed to test which color of light was most effective as a night interruption. The rationale was that effectiveness of different colors should indicate absorption characteristics of the pigment system involved in photoperiodism and help in its identification. The first step toward identification of the photoreceptor was to grow plants on short days and expose them to light of different colors near the middle of the night. Some exploratory experiments were done in the greenhouse and its adjacent rooms equipped with lamps whose light was filtered through different-colored glass. The fixtures used to apply the different colors of light were quite primitive by today's standards. One that was still in storage when this author did postdoctoral research with Borthwick and Hendricks (1961–1963) could be described as an oversized soup can with a lamp holder at the top and an approximately 6×6 in. square hole at the bottom. The 6×6 in. glass filters were of various colors, including red, yellow, blue, etc.

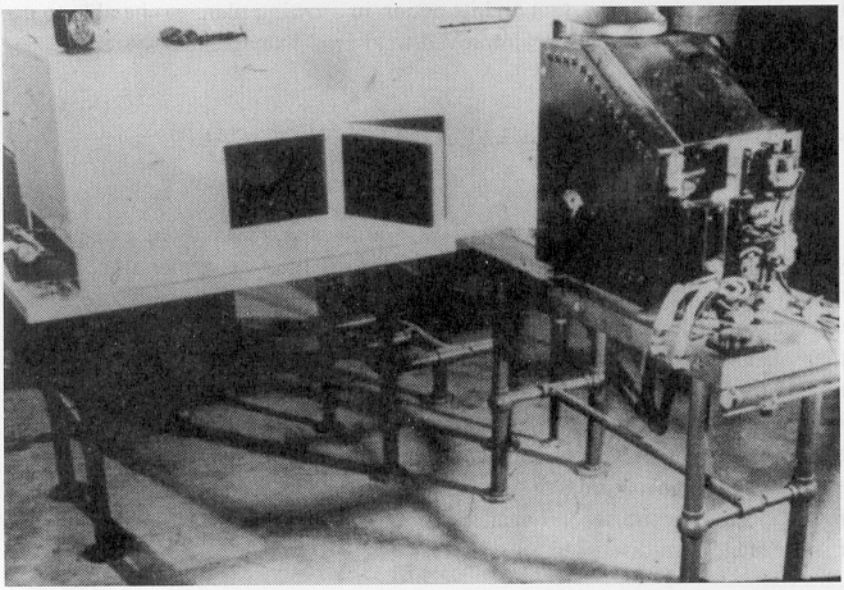
More refined experiments were done with plants grown for 8 hr per day in the carbon arc–illuminated growth room. They were given middle-of-night treatment for different durations under the different colors in adjacent rooms. An advantage of using the growth room was that the schedule could be arranged so that the middle of night for the plants occurred during the work day, so that the scientists could be present to apply more extensive treatment combinations. These experiments indicated that red was the most effective color; the information also suggested some characteristics of the photoreceptor that controlled photoperiodism. However, they still needed a more refined spectral response curve. At that point they enlisted help from Sterling Hendricks (a physical chemist who was interested in botany). Together, they decided that the ideal approach would be to treat plants with the various colors of the spectrum, as would be received

if white light was passed through a prism. This led to design, construction, and use of one of the most successful scientific instruments ever developed. The Beltsville Spectrograph was built in the mid-1940s primarily from spare and borrowed parts (15). Basically, the light source was a discarded (surplus) 12 kW carbon-arc projector that was used to light the stage of a nearby vaudeville theatre in the early 1900s (Fig. 2). The light was beamed through two large prisms that were once used by Samuel Pierpont Langley (1834–1906), a noted physicist, astronomer, and aeronautics pioneer. The prisms were considered historic and were already at the Smithsonian Institution, from which Hendricks borrowed them for an "indefinite" period (he borrowed them in the 1940s and returned them when he dismantled the spectrograph shortly before he retired in 1970).

Preliminary experiments with soybean demonstrated that the plants could be trimmed to a single recently expanded leaflet and still be responsive to red light in the middle of the night. This allowed the treatment of each test plant in a relatively narrow part of the spectrum that was projected onto a treatment table. The first action spectra showed a relatively broad (about 640- to beyond 660-nm) red action peak for control of flowering of both short-day and long-day plants (15–17). Photoreversibility of the effect of red light (R) by exposure to far-red (FR) was discovered in experiments with germination of light-requiring lettuce (*Latuca sativa* L.) seed in 1952 (18). The action peaks determined on the spectrograph indicated a R action peak at about 660 nm and a FR action peak at about 730 nm for seed germination. After discovery of photoreversible control for seed germination, photoreversible control of flowering was also documented (19). From these experiments, they concluded that a photoreversible pigment system existed in seeds and in growing plants. Further, they found that one form absorbed R and became the FR-absorbing form which then absorbed FR and became the R-absorbing form, etc. They concluded that the FR-absorbing form was biologically active in the germination of light-requiring seed and in photoperiodic control of flowering.

Their next proposed steps were to extract the photoreceptor and study its chemistry. W. L. Butler (a physicist), K. H. Norris (an instrumentation engineer), and H. W. Siegelman (a chemist) joined Hendricks for that phase. They grew corn (*Zea mays* L.) seedlings in darkness and measured change in optical density following brief exposure to R, then FR, then R, etc., on an instrument built by Norris. The changes in optical density were used as an indication of concentration of the photoreversible pigment hypothesized to control germination and flowering. The resulting paper by Butler et al. (20) was published in the *Proceedings of the National Academy of Sciences of the United States of America* in 1959, and it was soon recognized as the discovery of phytochrome.

Soon after the discovery of phytochrome by the Beltsville group, this author arrived to do postdoctoral research with Drs. Borthwick and Hendricks. Although emphasis of the lab was on chemical characterization of phytochrome



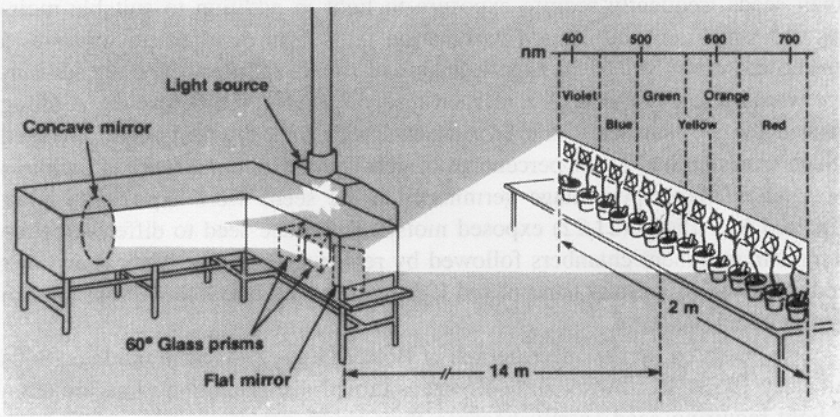


Figure 2 Photograph of the carbon arc projector (light source) and the opening from which the ''rainbow of colors'' emerged (top), and a diagram of the spectrograph showing the light path from source to treatment table.

(which was then assumed to be the same in all plant species and the same in all stages of growth), my interest was in whole plants. My goal was to learn enough about the phytochrome system and its action in growing plants to be able to use that information in developing improved field-crop management systems.

IV. PHYTOCHROME-REGULATED PHYSIOLOGICAL RESPONSES

It is evident that phytochrome functions in a number of stages in a plant's life cycle to aid its survival and the reproduction of the next generation. Several critical phytochrome-regulated stages in the life of annual plants are during germination of light-requiring seed, sensing and adapting to competition from other plants, and season recognition resulting in development of an adequate number of ripe seed before freezing or other unfavorable weather occurs. In biennials, such as sweetclover (*Melilotus officinalis* L.), there is a period of vegetative growth of shoots followed by a period during which storage roots develop rapidly in autumn of the first year, followed by flowering and seed production during the second year. Examples of phytochrome function in each of these stages are discussed.

A. Seed Germination

Small seeds frequently require exposure to light in addition to suitable moisture and temperature to trigger germination. This light requirement serves as a protective mechanism, because germination of small seeds far below the soil surface would result in exhaustion of food reserves in the seed before the seedling reached the soil surface. Early experiments with light-requiring seed involved lettuce seed that had a low percentage of germination in uninterrupted darkness but a much higher percentage germinated if the seeds were exposed to light. Flint and McAllister (21,22) exposed moistened lettuce seed to different colors of light in treatment chambers followed by return to darkness. They found that seeds exposed to a broad band of red light germinated better than those kept in uninterrupted darkness.

As research on the spectrograph at Beltsville progressed in the late 1940s and early 1950s, Borthwick and colleagues turned their attention to germination of light-requiring seed (partly because they could get more data points from small seeds than from large soybean plants when arranged in the spectrum on the treatment table). The lettuce seeds were aligned in rows (on moist paper in plastic boxes) and exposed to the various colors on the spectrograph, followed by return to darkness for a few days before the germinated seed were counted. Seeds that received red light germinated best, but it was also found that seeds

exposed to wavelengths just beyond visible red light sometimes had a slightly lower germination percentage than the dark controls. This was followed by an experiment in which all seeds were exposed to bright light before treatment on the spectrograph. After such treatment, rows of seeds that were treated in the red band had high germination percentages; those in the rows just beyond visible red (now called far-red) had much lower germination percentages. The Borthwick-led team then treated seed under broad-band fixed filters where they found R-FR photoreversible control (Table 1). That 1952 paper by Borthwick et al. (18) was the first report describing the photoreversible control of a morphological response (germination) and was a key step in the discovery of phytochrome (discussed earlier in this chapter).

About 12 years later, while working to develop uniform tobacco transplants that were suited to mechanical transplanting, I looked into the light requirement for germination as a possible contributor to the unpredictable germination and nonuniformity among seedlings started in traditional outdoor starting beds. Tobacco seeds are very small (about 11,000 seeds per gram), and seedlings must be protected until they are large enough to be transplanted to a field. The first step was to determine the uniformity (or nonuniformity) of the light requirement among varieties and among different seed lots from a given variety (Table 2). Quite clearly, the results showed that there was much variability (among the varieties and even within the same variety) in the percentage of seed that germinated without any light. This was an immediate explanation of a cause of nonuniformity in seedling establishment in conventional starting beds, in which some of the seeds were covered with a thin layer of soil (23). However, more information was needed to remove the problem. Totally light-requiring (LR) and

Table 1 Germination of Grand Rapids Lettuce Seed in Response to Repeated 1-Min Irradiations with Red (R) Alternated with 4-Min Irradiations with Far-Red (FR) Light

Irradiation	Germination (%)
None (dark control)	9
R	98
R, FR	54
R, FR, R	100
R, FR, R, FR	43
R, FR, R, FR, R	99

Source: Adapted from Ref. 18.

Table 2 Germination of Randomly Selected Seed Lots of (A) Five Different Burley Tobacco Varieties, and (B) Five Different Seed Lots from One of the Varieties in Light or in Uninterrupted Darkness at 20°C

	Germination (%)	
Sample	In darkness	In light
(A) Different varieties		
Burley 21	48[a]	94
Burley 37	53	95
Ky 10	6	99
Ky 12	3	99
Ky 16	5	98
(B) Different seed lots of Burley 21 from greenhouse and field		
Plant 1, greenhouse	56	—[b]
Plant 2, greenhouse	30	—
Plant 3, greenhouse	39	—
Lot 1, field	68	—
Lot 2, field	76	—

[a]Data are means for 5 lots of 100 seed each.
[b]Germination of the Burley 21 seed lots in light ranged from 94 to 99% at 20°C.
Source: Adapted from Ref. 23.

light-indifferent (LI) lines were developed through a recurrent selection procedure (24). Progeny of self-pollinated and reciprocal cross-pollinations showed both genetic and maternal control (24). The LR and LI lines were used in many experiments, including germination under (and emergence from) different depths of black or brown soils (25). LR and LI seed on the surface of the soils germinated 99.6 and 98.2%, respectively. LI seed germinated and emerged from below as much as 8 mm of moist black or brown soil, indicating that the energy reserve in the tiny seeds was adequate for survival of seedlings during emergence from that depth. However, less than 1.5% of the LR seeds emerged from a depth of 2 mm and none emerged from 4 mm or greater depths, indicating that a very thin layer of moist black or brown soil blocked the light required to trigger germination of the LR seed. These results indicated that the LR seed should be germinated on the surface of moist soil to obtain high percentages.

Another possibility was to precondition the phytochrome system in the LR seeds to satisfy the light requirement before sowing them. After determining that the light requirement could not be satisfied by exposing dry LR seed to

light, seeds were placed on moist paper in petri dishes and kept in darkness at 20°C for 50 hr before giving brief exposures to R or FR. In that scenario, seeds that received 5 min of R and then returned to darkness germinated about 99%. Those that received 5 min of FR immediately after the R did not germinate, indicating phytochrome involvement. In an attempt to precondition the phytochrome system, some of the seeds that received 5 min of R and others that received 5 min of R followed by 5 min of FR were air-dried in darkness immediately after the end of the R or FR treatment. The dried seeds were stored for various durations and then tested for germination. Those that received R before being dried germinated at high percentages after being placed on moist paper (in darkness). Those that had received R followed immediately by FR before drying did not germinate when placed on moist paper in darkness after a period of storage. Also, seeds that had received R before they were dried and stored did not respond to FR applied while they remained dry. Apparently the hydrated phytochrome was responsive to light and the dehydrated phytochrome in the LR seeds was not responsive to either R or FR. Although these studies were done with tobacco seeds, the information on preconditioning the phytochrome system in light-requiring seeds may become useful in spaced sowing of pelleted seeds.

B. Season Recognition

Biennial plants begin growth during one year and complete their life cycle the next. For example, sweetclover, a legume used as a soil-improvement crop, begins growth in spring and produces erect stems with abundant foliage during the long days of late spring and early summer. During the decreasing day lengths of autumn, shoot growth seems to stop and taproots enlarge rapidly, while they also develop vegetative buds near the soil line (26). The following spring, the crown buds develop into rapidly growing shoots that flower, produce seed, and die. Clearly, the plants recognize seasonal environment changes and respond morphologically.

Sweetclover taproots with developing crown buds collected at monthly intervals in an Iowa field from mid-August to mid-November are shown in Figure 3. During that 3-month period, natural photoperiods decreased from nearly 14 hr to less than 10 hr, and mean daily temperatures decreased from about 22°C (about 72°F) to near freezing (Fig. 3, top). At time of the mid-August root collection, other plants were transferred (in blocks of soil) to a soil bed in a greenhouse with natural day lengths and minimum temperature of 22°C until mid-November, when the greenhouse-grown taproots were compared with those that had been exposed to natural day lengths and natural temperatures in the field. Taproots were about the same size and with the same amount of crown buds at both locations in November (Fig. 4), indicating that photoperiodic control dominated this aspect of season recognition and morphological development (27).

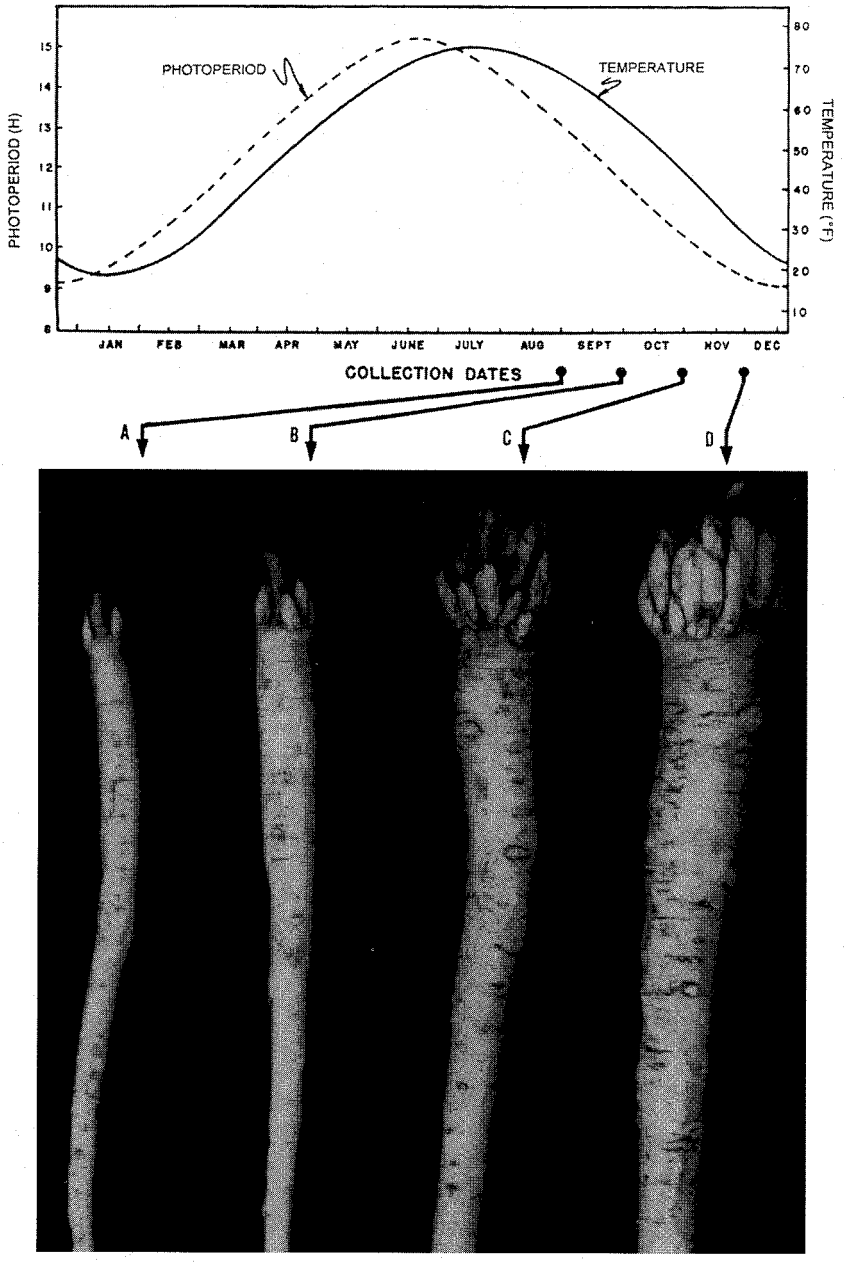


Figure 3 Mean natural photoperiods and temperatures (top) and first-year biennial sweetclover taproots sampled from a field near Ames, Iowa, at monthly intervals from mid-August to mid-November. (Adapted from Ref. 26.)

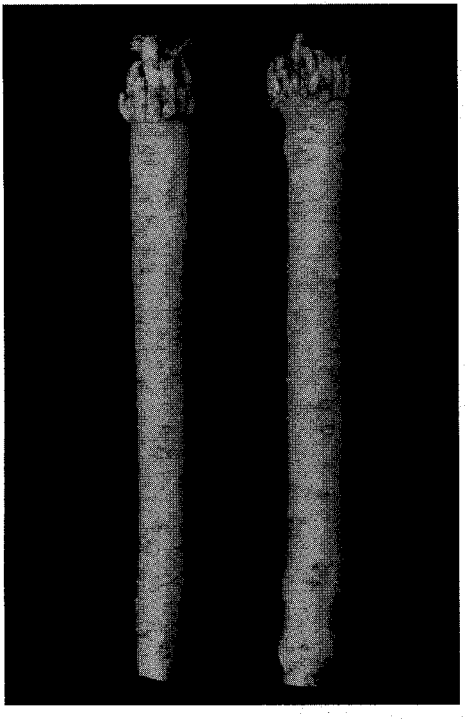


Figure 4 Sweetclover taproots from first-year biennial plants grown on natural photoperiods, and with natural temperatures (left) and 22°C minimum temperature (right) until mid-November. (From Ref. 27.)

When first-year sweetclover plants were exposed to photoperiods ranging from 9 to 24 hr per day in a greenhouse from time of emergence, those on 9-hr days developed only low-growing shoots but large fleshy taproots (Fig. 5). Conversely, those on continuous light grew taller and flowered within 3 months without ever developing fleshy taproots. Clearly, photoperiod signaled the plants on 9-hr days to get ready for winter and signaled those on continuous light that there was no need to invest resources in developing taproot reserves.

Annual plants include many crop plants and many weed species. Growth patterns of plants such as soybean, tobacco, and cocklebur were discussed earlier in this chapter, because recognition of their seasonal responses contributed to the discoveries of photoperiodism and phytochrome. In nature the greatest survival advantage in terms of number of seed produced per plant is generally favored by flowering late enough for the plant to develop a large photosynthetic area to support many developing seeds but early enough so that the seed ripen

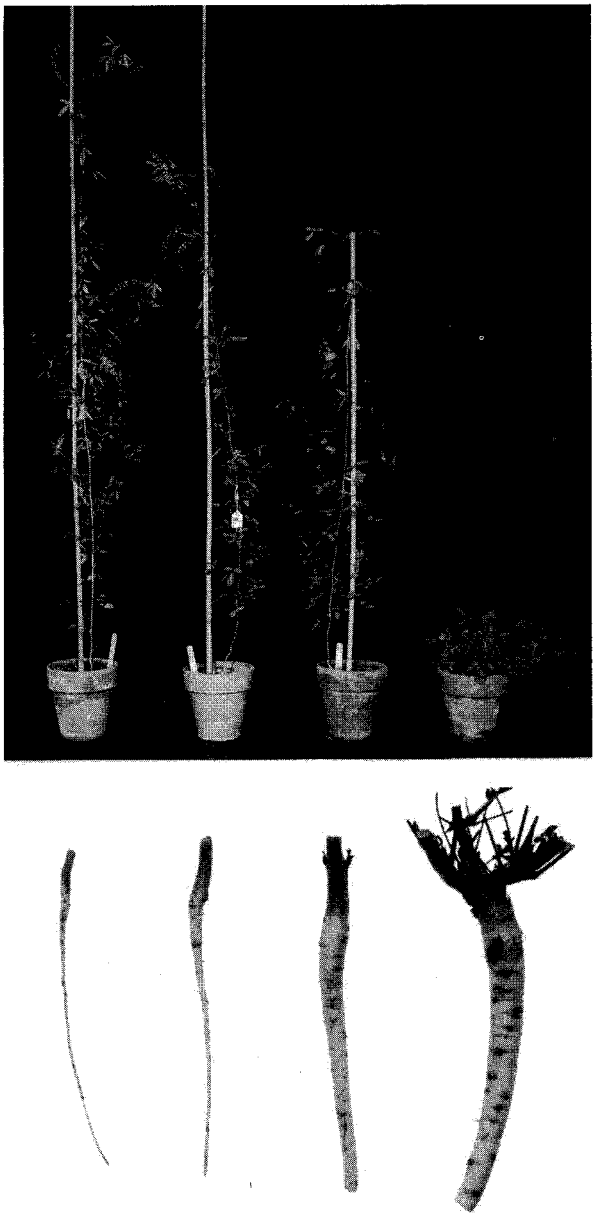


Figure 5 Shoots (top) and taproots (bottom) of first-year biennial sweetclover plants grown for 100 days (from germination) on (left to right) 24-, 20-, 16-, and 9-hr photoperiods in a warm greenhouse. (From Ref. 27.)

before being exposed to freezing weather. However, in mechanized crop production systems, greater yield per hectare may be achieved by increasing the plant population density to the point where yield per plant is decreased.

In some cases, a plant's response to photoperiod differs with temperature (28,29). For example, a problem encountered by many Burley tobacco farmers who started their plants in protected outdoor starting beds was that some plants flowered early (undesirable) and at a small size after being transplanted to the field, if the seedlings had been exposed to a week or more of overcast weather in the starting bed just before being transplanted. During such periods of overcast weather, the seedlings usually received cool temperature and decreased light intensity.

Controlled environments were used during the pretransplant period to determine the cause of such premature flowering. Seedlings became florally inducted during the pretransplant period, when they received 8 hr of bright light alternated with 16 hr of uninterrupted darkness at 18°C each day for about a week. The same floral response was obtained with "natural" day lengths and decreased light intensity at 18°C. However, plants started at the same time from the same lot of seed remained vegetative if given 8 hr of bright light alternated with 16 hr of uninterrupted darkness at 28°C. Some typical results from controlled environments are summarized in Table 3.

Table 3 Post-transplant Floral Responses of Burley Tobacco to Photoperiod, Temperature, and Light Intensity Received During the Last 10 Days of the Pretransplant Period

Photoperiod		Temp.	Treatment		Early flowering
(Hours)	(μmol $m^{-1}s^{-1}$)	(°C)	(Light)[a]	(Heat)[b]	%
8	520	18	no	no	100[c]
8	520	28	no	no	0
8	520	18	yes	no	0
8	520	18	no	yes	0
13.5	100	18	no	no	33
13.5	100	18	yes	no	0
13.5	520	28	no	no	0

[a]Low-intensity red light was applied for 5 min in the middle of each night.
[b]Temperature was raised to 38°C for 2 hr in the middle of each day.
[c]Percentage of plants that flowered within 30 days after being transplanted to the field in contrast to about 60 days for controls (the early flowering resulted in fewer than 10 leaves per plant versus about 28 for controls that were not florally inducted during the pretransplant period).
Source: Adapted from Refs. 28 and 29.

At 18°C the seedlings responded as typical short-day plants. That is, 5 min of R in the middle of the 16-hr night inhibited flowering, and 5 min of FR immediately after the R reversed the inhibitory effect of R. In an attempt to mimic conditions from the outdoor starting beds, some tobacco seedlings that were large enough to become florally inducted on 8-hr 18°C days received several hours of elevated temperature (about 38°C) in the middle of the day to provide a period of warming as would occur on sunny days. The brief period of elevated temperature had the same inhibitory effect as a middle-of-night exposure to R. Later, it was found that the period of elevated temperature could be applied earlier or later during the day and even during the night. Clearly, temperature influenced the floral response of the Burley type of tobacco to short days. The practical problem concerning the cause of early flowering was solved but the light-temperature-phytochrome interactions in the season-sensing control mechanism are yet to be resolved.

V. PHYTOCHROME SENSING OF COMPETITION

An unexpected observation can be the beginning of a discovery. For example, as a boy on a farm in Iowa in the 1940s, I observed that newly emerged weed seedlings growing close together grew taller and were easier to pull (i.e., they had less massive roots) than those that were farther apart. That stem elongation response to nearness of other plants was evident even before mutual shading occurred, and the same response to nearness of other plants also occurred with seedlings of crop plants such as bean. It appeared that the seedlings were receiving a signal to outgrow their competitors. I asked why seedlings responded in this manner, but no one had a realistic answer at the time.

A possible answer began to evolve years later, when I was a postdoctoral researcher with Drs. Hendricks and Borthwick at the Pioneering Research Laboratory for Plant Physiology at Beltsville in 1961–1963. That was about 2 years after the group had discovered phytochrome, and most of our experiments on the Beltsville Spectrograph involved middle-of-night treatment of tiny test plants (*Chenopodium rubrum* L.) to determine energy requirements for conversion of phytochrome to the "biologically active" form and dark reversion times in phytochrome control of flowering (those experiments contributed background for development of cyclic lighting for control of flowering—which is now a standard practice in the floral industry). However, observation of an unexpected morphological response that was not part of a planned experiment became a key in answering the question about seedling stem-elongation responses to competition from other seedlings.

After many middle-of-night treatments of test plants on the spectrograph to learn more about phytochrome control of flowering (14), we decided to treat

seedlings on the spectrograph at the end of various lengths of day given in the carbon-arc growth room. The objective was to determine whether we could adjust the photoequilibrium between Pr and Pfr enough at the beginning of the night to affect the "critical day length" for flowering. Results of the planned part of the experiment were not dramatic, but an unexpected observation was a stem elongation and raised leaf angle response to FR at longer wavelengths than were thought at that time (1962) to have any influence via phytochrome. A pencil notation of the observed seedling growth response at 750 to 770 nm (well beyond the Pfr absorption peak of 730 nm) on the spectrograph became a critical step in understanding phytochrome sensing of competition in sun-grown plants in the late 1960s and in development of the "ideal" reflection spectrum used in development of colored mulch technology in the early 1990s (discussed in a "Commentary" entitled "Phytochrome regulation of morphogenesis in green plants: From the Beltsville Spectrograph to colored mulch in the field") (7).

A. Controlled Environments and Plant Spacing

Many experiments were done in controlled environments to test morphological responses to R and FR. For example, Downs et al. (30,31) reported photoreversible control of elongation of pinto bean (*Phasoleus vulgaris* L.) as part of the work leading to discovery of phytochrome by Butler et al. (20). Subsequently, there were many reports from many labs showing photoreversible control of various morphological responses.

Work with pretransplant-size tobacco seedlings in controlled environments and in outdoor protected starting beds combined the lab and field approaches that showed the importance of FR during the day on phytochrome-regulated plant morphological development in the field. Although it was well known among tobacco farmers that closeness of seedlings in outdoor starting beds could influence stem length and root size (32), the competition-sensing mechanism was unknown. In 1964, experiments were initiated with tobacco to determine the relationships among plant spacing, FR, and development of stems, leaves, and roots as a background for possible development of large-scale greenhouse production of transplants. Another objective was to determine whether the light environment during the pretransplant period would affect plant growth after the seedlings were transplanted to the field. The goal was to "tailor make" transplants to be predictably uniform in size and in their growth response to the field environment. It was obvious that extra FR during the day (especially near end of day) in the controlled environments resulted in seedling stem and root characteristics very similar to those of close-spaced seedlings (5,28,29). However, the portable spectroradiometer available at the time was too large to measure light spectra among closely spaced seedlings in the starting bed. Nevertheless, the

raised leaf angle, lighter green color, and stem elongation responses of close-spaced seedlings were very similar to those of plants that received extra FR in the controlled environment and to responses of the chenopodium seedlings to FR at 750 to 770 nm as observed on the Beltsville Spectrograph in 1962 (discussed in Sec. V, above). The close-spaced seedlings and those that received extra FR in the controlled environment had less massive roots than wide-spaced plants or those that received R. The effects of FR could be negated if a brief exposure to R was applied immediately after the FR, indicating photoreversible phytochrome regulation of shoot/root size relationship in the seedlings (5). Results from the controlled environment and the morphological responses to closeness of other seedlings in the outdoor starting bed suggested that the elongation response to nearness of other seedlings was due to elevated FR and that the FR/R photon ratio was the important variable in field plant recognition of potential competition from other green plants (5). In addition to developing longer internodes, heavier stems, and less massive roots in response to extra FR, plants developed leaves with longer midveins and less biomass per area of leaf lamina. Leaves that developed when plants received the higher FR/R ratios also fixed more CO_2 per mass of leaf, and they had higher concentrations of sugars in leaves and stems (33,34). Chloroplast ultrastructure also differed. Chloroplasts from leaves that developed with the higher FR/R ratio had more grana with fewer thylakoid layers per granum (35). They also had fewer and smaller starch grains but greater sugar concentrations. These results suggested phytochrome involvement in the development of the photosynthetic apparatus and in carbon partitioning at the cellular level (35–37).

The R-FR photoreversible control of the chemical and morphological responses listed above suggested that a high FR/R ratio (a low Pfr level) functioned in metabolic events that affected photosynthate partitioning, resulting in longer stems and less new root growth (5). Nevertheless, results did not indicate whether a low level of Pfr initiated a chain of events leading to "competition adapted" development or whether the events happened because the level of Pfr was too low to signal events leading to "sun adapted" characteristics (33). Those authors also suggested that some unrecognized factor other than Pfr level associated with the FR/R photon ratio might affect morphogenesis in the growing plants. Whatever the mechanism of action, it was quite clear that FR was a dominant factor in signaling the initiation of morphological responses that might have survival value among close-spaced plants (5,33,35). That is, partitioning more photosynthate to development of a longer stem should increase the probability that a plant could keep some of its leaves in sunlight above the competing plants. Also, leaves that are more efficient photosynthetically might favor survival if the amount of photosynthetic light received was decreased by shade from competing plants.

B. FR Reflection from Green Plants

Spectrophotometric measurements of light in and near a canopy of large tobacco plants in 1967 supported the concept that FR transmitted through and/or reflected from nearby green leaves affected the FR/R ratio sufficiently to obtain the "close spaced" plant characteristics. Spectral measurements taken at 11 narrow wavebands from 391 to 686 nm and at 725 and 791 nm in the FR region are shown in Table 4. The percentages shown in the table are relative to values received at the same wavebands in incoming sunlight on a road away from the green plants (to avoid possible influence of reflected FR changing the values measured as incoming light). The values at 791 nm were about 15% greater in sunflecks on the soil near tall tobacco plants than in sunlight on the road surface. Also, notice in the table that values at 791 nm are greater than those at 725 nm, which is near the absorption peak for Pfr. The significance of that

Table 4 Percentages of Incoming Sunlight Received at Various Wavebands Within and Below a Canopy of 190-cm Tall Tobacco in a Field Near Lexington, Kentucky, at About 1 p.m. on September 1, 1967

Peak wavelength (nm)	Percentage of incoming sunlight[a]		
	Within canopy	Below canopy	Below a single leaf
391	0.9	0.5	1.7
432	0.7	0.3	0.5
448	0.7	0.3	0.7
483	0.6	0.4	0.9
511	0.8	0.6	3.3
543	11.0	6.5	22.7
576	5.0	3.4	14.7
601	2.6	2.1	10.8
629	1.7	1.4	7.9
658	2.3	1.7	6.1
686	2.2	1.9	6.6
725	11.6	8.8	27.5
791	36.3	20.3	49.5

[a]Incoming sunlight was measured on a road, away from the tall plants. The value at 791 nm was about 15% greater in sunflecks on the ground near tobacco plants than it was on the road, away from large plants.

Source: Adapted from Ref. 5.

difference became apparent in 1983, when canopy spectral measurements were made at 5-nm intervals from 400 to 800 nm (see below).

In 1983, I became aware of experiments by P. G. Hunt and colleagues on sandy soils with low water-holding capacity in South Carolina. They obtained higher soybean yields in north-south oriented rows when irrigated and higher yields in east-west rows when there was occasional water stress. In an early discussion, we hypothesized that such a response pattern could occur if something associated with north-south row orientation caused plants to put more growth in shoots and less in roots. I recalled some controlled-environment experiments in which more FR and a higher FR/R photon ratio acted through the phytochrome system to allocate more growth to shoots and less to roots (5). We then measured reflection at 5-nm intervals from 400 to 800 nm from green soybean leaves and found that the reflection reached maximum percentage at about 750 to 760 nm (Fig. 6). This was the same waveband in the FR range that resulted in altered stem and leaf morphology on the Beltsville Spectrograph in 1962 (see discussion in Sec. V). We also measured the spectra of light coming to the upper parts of soybean plants growing in north-south versus east-west rows. We found

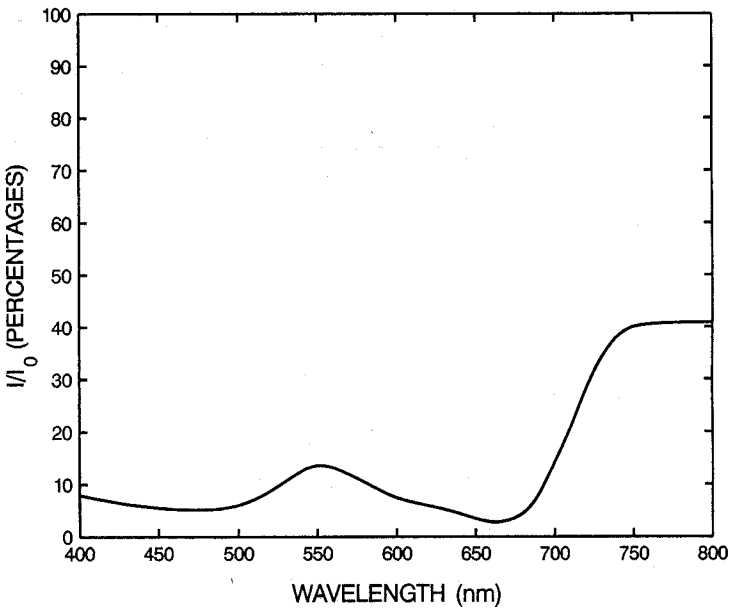


Figure 6 Spectrum of light reflected from the upper surface of a fully expanded field-grown soybean leaf (the curve shows percentages reflected relative to the quantity of incoming light at 5-nm intervals). (Adapted from Ref. 7.)

that those in north-south rows received more FR reflected from adjacent rows and higher FR/R photon ratios near the end of day (6). This was attributed to the heliotropic (sun-tracking) leaves functioning as directional FR reflectors. A companion controlled-environment experiment with the same variety of soybean did indeed allocate more growth to shoots and less to roots if they received a higher FR/R ratio at the end of each day (6). The experiment was repeated with southern pea (*Vigna unguiculata* L) , which also has heliotropic leaves and directional reflection of FR. Experiments with wheat (*Triticum aestivum* L.) and corn (neither has heliotropic leaves) showed high morphological responses to nearness of neighbor plants but not to row orientation (38,39). These and many other experiments have shown that FR reflected from green leaves of nearby plants affected the FR/R ratio enough to act through the plants' natural phytochrome system to affect morphology and yield (40,41). Hence, effects of reflected FR and its action through the phytochrome system should be considered in developing new crop-management systems that involve innovative plant spacing and row orientation.

C. Reflection from the Soil Surface

After it was apparent that plants growing outdoors responded morphologically to FR reflected from nearby growing plants (6,38), we wondered whether growing plants would also respond morphologically to spectral differences reflected upward from different colored soils or from dead plant residue left on the soil surface, as in a conservation tillage system. Upward reflection from different colored bare soils and from the different colored soils that were partially covered (about 80%) with dead plant residue were measured in 1984 and 1985 (42). The upward reflections were measured 10 cm above the surface because that is within the seedling establishment zone, and young seedlings are morphologically very responsive to reflected FR (38,40,41). The working hypothesis was that plants growing in sunlight would be influenced morphologically by the wavelength distribution (particularly the amount of FR and the FR/R photon ratio) in upwardly reflected light, just as they respond to FR reflected from nearby growing plants. That is, plants growing over materials that reflected a FR/R ratio higher than the ratio in incoming sunlight (at the same time and place) would develop larger shoots and a higher shoot/root biomass ratio, whereas plants that received a lower FR/R ratio in the reflected light would develop a lower shoot/root biomass ratio. To test the hypothesis, we grew seedlings of soybean (43), cotton (*Gossypium hirsutum* L.) (44,45), and other plants in large pots on a greenhouse bench. A 48 × 48 in. polystyrene foam panel with equispaced 2-in. holes was placed over each group of five pots, and each panel was covered with different colored soils or plant residue. This procedure allowed study of plant response to soil surface color while rhizosphere temperature (in the pots below the insulation

panels) was the same below all surface colors within an experiment. Seedling shoot and root growth responses to the FR/R ratio in upwardly reflected light were as hypothesized (5,42). When it was apparent that sun-grown seedlings of the different crop plant species all responded to wavelength distribution in upwardly reflected light over different colored soils and plant residues in the greenhouse, the studies were expanded to include painted panels. In addition to allowing a wider selection of colors, the painted panels were better suited for outdoor experiments because the different colored soils and dead plant residues were easily blown away. The important point was that seedlings responded in the same way to a given reflection spectrum whether they were over painted or soil-covered panels (44). Following many outdoor experiments with painted panels, it became obvious that plants did not always respond in the same way to a given color, such as red. After the initial observation of different morphological responses to the "same color," we measured reflection spectra from several different batches of red paint and found that even though reflection was almost identical in the visible range (400 to 700 nm), there were differences in the FR range (700 to about 800 nm) and in the FR/R photon ratios reflected from the surface. This provided evidence that two or more batches of a given color could appear identical to human vision while reflecting a distinctly different FR/R ratio and could have quite different morphological effects on the growing plants. Following that experience, we concluded that a reflection spectrum from each batch of paint was needed before plant response to a given color could be interpreted. This observation carried through to development of colored mulch technology (described below).

VI. COLORED MULCH TECHNOLOGY

Development of colored mulch technology was a natural progression from the research with plants growing in sunlight over panels with different surface colors, as described above. Use of exterior enamels to provide the different panel surface colors was an economical and convenient approach for obtaining a range of reflection spectra for small plots. Because the visible and FR parts of the spectrum were both important for plant growth, it was necessary to know the reflection spectrum for each batch of paint before we could interpret the plant growth responses. The approach with painted panels was to allow plants to grow in summer sunlight for photosynthesis and to use a reflected FR/R photon ratio to act through the natural photomorphogenic pigments (primarily phytochrome) within the growing plant to regulate partitioning of the photoassimilate to developing roots, shoot, and fruit. The working hypothesis (based on previous observations of seedling growth responses to FR at 750 to 760 nm on the Beltsville Spectrograph, experiments in controlled environments, reflection from nearby

growing plants, upward reflection from different colored dead plant residue, and reflection from painted panels) for use of different colored panels in sunlight was that an upwardly reflected FR/R photon ratio higher than the ratio in incoming sunlight would signal the plant to allocate more of its new resources to shoot (including fruit) growth, while a FR/R ratio lower than that in the incoming sunlight would favor root growth.

In 1986 D. R. Decoteau, who was a new horticulturist at the Clemson Pee Dee Research Center at that time, asked if he could join in for a field test with trickle-irrigated tomato (*Lycopersicon esculentum* Mill.). It was an ideal choice, because we had already tested R-FR photoreversible control of allocation of photosynthate in tomato and other food-crop seedlings in a controlled environment. In that experiment, all seedlings were of the same age and received the same amount of photosynthetic light. Nevertheless, those that received a brief exposure to FR (a higher FR/R photon ratio) at the end of each day had larger shoots and a higher shoot/root biomass ratio than those that received R (a low FR/R ratio). Shoots of seedlings that received a brief exposure to R immediately after the FR remained smaller and appeared the same as those that did not receive the FR treatment. This strong photoreversible control of seedling morphogenesis by phytochrome indicated a high probability that sun-grown tomato plants would be responsive to the FR/R photon ratio reflected from the soil surface.

The experiment that contributed greatly to early stages of the colored mulch technology was relatively simple. Standard black plastic mulch was placed over trickle-irrigation tubes in raised-bed field plots. A range of upwardly reflected spectra was obtained by painting some of the plastic with exterior enamel. Subplots were painted red or white and some were left as unpainted black (controls). These colors were selected because black plastic mulch (over trickle-irrigation tubes) was widely used in commercial tomato production to conserve water, control weeds using less herbicides, and keep fruit clean. Red and white were used because of our previous experiments with small painted insulation panels (discussed above). The red paint that we used reflected a higher FR/R photon ratio than was present in incoming sunlight at the same time and place, whereas the white paint reflected much more photosynthetic light than the red paint but a FR/R photon ratio very similar to the ratio in the incoming sunlight. Soil temperature was cooler under white-painted plastic but very similar below red and black. The basic experiment was conducted for 2 years and in two locations. The early-crop tomato yields were 12 to 20% higher over red than over the standard black (control) (46). Early crop yields over the white surfaces were lower than those over black or red. In follow-up experiments, we found that yields sometimes differed over different batches of red paint. All of these observations contributed to the development of the colored mulch technology.

Patent applications were filed and the technology was licensed by a major manufacturer of plastic mulch. The next step was the development of a "theo-

retically ideal'' reflection spectrum for yield of tomato, strawberry (*Fragaria* × *ananassa* Duch.), and other small fruit crops. Pigment combinations that reflect the ''ideal'' spectrum were incorporated into plastic sheets and are now available to large- and small-scale growers as selective reflective mulch (SRM-red). Other colors are in development for enhancement of flavor and quality of food crops.

A. Tomato Fruit Yield

Early-crop tomato yields over clean, intact sheets of the specially formulated red plastic mulch (over trickle-irrigation tubes) were consistently higher than those over standard black plastic (47). In that series of experiments, it was found that the photodegradable red plastic used in 1994 was effective only while it remained intact and capable of reflecting to the developing tomato fruit and the nearby parts of the growing plant. Also, the yield advantage over the photodegradable red versus standard black plastic returned after the degraded red plastic was replaced with a new intact layer of the red plastic (47).

Yields over the light-stable red plastic used in 1995 (and thereafter in our experiments) were consistently superior to those over standard black plastic (47). Several important aspects of the colored mulch technology became apparent in those experiments with tomato: (a) the mulch surface had to reflect a wavelength combination that could act through photomorphogenic pigments within the plant to cause allocation of more photoassimilate to developing fruit, (b) the reflecting surface had to remain intact to reflect its morphogenic light signal to the developing fruit for the entire season, (c) spray residues or dust on the mulch surface altered the spectrum reflected from that surface and made it ineffective, and (d) both increased number and size of fruit per plant contributed to the early-crop tomato yield increases with the red versus standard black plastic mulch.

B. Strawberry Fruit Yield

Like tomato, strawberry fruit yields were greater over the specially formulated red versus the standard black plastic mulch in raised-bed, trickle-irrigated field plots (48). The light-stable formulation from 1995 was used in the 2-year two-location test. The enhanced yield over the red mulch resulted primarily from larger berries. It is of interest that the percent increase in size of strawberries grown over red versus black plastic was greater than the percent increase in size of tomatoes grown over red versus black (47,48). A possible explanation is that strawberries are closer to the reflecting surface during fruit development. This explanation is consistent with the seedling stem elongation response to nearness of other growing (FR-reflecting) plants, as discussed earlier in this chapter. If this

interpretation is correct, one should expect diminishing effect on size per fruit as distance of the developing fruit from the red mulch increases. For example, strawberry size per fruit should be influenced more percentagewise than tomato, but tomato should be influenced more than a tree fruit if the red reflector was the same size and on the soil surface in all of these examples.

C. Quality of Plant Products

In addition to effects of morphogenic light reflected from colored mulches (specially formulated plastic or painted panels) on yield and on individual components of yield, it is already evident that light reflected from colored mulches can alter flavor, nutrient, and other quality characteristics of plant products. For example, a few years ago we used turnip (a root crop) to determine whether reflection from different colored mulches could affect the shoot/root biomass ratio in sun-grown plants in field plots. Although cotton and corn were used in preliminary experiments with potted plants in the greenhouse, turnip (*Brassica rapa* L.) was suggested as the species of choice for the field test by the person who realized he would be responsible for digging up the roots. After weighing the turnip shoots and roots from a number of field plots, it was obvious that plants that received a higher FR/R ratio in reflected light developed larger shoot/root biomass ratios, and vice versa. At that point, we temporarily stopped weighing to determine whether the flavor of the edible roots was altered by the color of mulch. Roots from the different colored (painted) mulches ranged from almost sweet to quite sharp in flavor as expressed by the majority of the 25 volunteer "taste testers." Roots from plants grown with blue mulch had the sharpest flavor, and those grown with green were mildest, even though both the blue and the green surfaces reflected about the same FR/R ratio and the plants had developed similar root size and shoot/root biomass ratios.

The next step was to do chemical analyses. Concentrations of flavor components such as glucosinolates and sugars in turnip roots were indeed affected by the color of light reflected to the growing leaves (49). Roots from plants grown with blue had the higher concentration of glucosinolates. This may be of more than academic interest, because it has been reported by Wattenberg (50) and others that certain glucosinolates or their derivatives may function as protective agents against carcinogens.

VII. SUMMARY

The growth and development of a plant are regulated by its genetics and the environment in which it grows. Genetic factors set the potential size and composition of the plant, but its growth environment determines the degree to which

that potential is attained. Light is a component of the environment that follows a generally predictable pattern year after year at a given geographic location. Light involvement in photosynthesis is well known and widely studied. However, photomorphogenesis is involved in the allocation and use of the products of photosynthesis in a manner that favors survival of the plant as it proceeds through its life cycle. Knowledge of the natural regulatory systems involved in photomorphogenesis is important in developing innovative strategies for crop improvement.

Phytochrome is an important photomorphogenic pigment system that signals seedlings when other plants are nearby and they must adapt to the competition; it also tells grown plants when to flower, so that the seed will have time to ripen before adverse weather sets in. Knowledge of phytochrome action in regulation of photoperiodic control of flowering has resulted in development of cyclic lighting, which is now used internationally to control time of flowering in the floral industry at a fraction of the cost of continuous lighting to extend photoperiod. Awareness that the phytochrome system in growing plants (especially seedlings) responds to FR reflected from nearby growing plants and that an increased FR/R photon ratio acts through the natural phytochrome system within the plant to allocate more growth to shoots is important in developing new field-crop management systems. For example, plant spacing, row orientation, and even the color of soil and dead plant residue on the soil surface can reflect morphogenic light patterns that affect yield and quality.

The accumulated information on phytochrome regulation of morphogenesis in controlled environments as well as the phytochrome-regulated growth response to FR reflected from nearby growing plants has led to development of colored mulch technology. Although other photoreceptors are involved in affecting some flavor and nutrient components in food crops grown over colored mulches, the FR/R photon ratio reflected from mulch on the soil surface to sun-grown plants can have a major impact on the allocation of new growth among developing roots, stems, leaves, fruit, and seed. An objective of the colored mulch technology is to retain the water-conservation, soil-warming, and weed-control benefits of standard black plastic mulch and to add the yield- and quality-enhancing benefits of reflected morphogenic light at little added cost to the grower. Enhanced yield of tomato and strawberry have already been documented over the red selective reflective mulch versus standard black plastic mulch, as have some effects on the flavor and nutrient quality of food crops. Many other experiments on yield and quality of shoot and root crops are in progress with red and a range of other colors versus standard black plastic mulch. The colored mulch technology has advanced during the last 15 years from a laboratory theory to reality in improving crop yield and quality, with worldwide implications.

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